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Acropora in Hawaii. Part 1. History of the Scientific Record, Systematics, and Ecology[1]

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ABSTRACT: Present occurrence of the coral genus *Acropora* in Hawaii has long been questioned. This paper reviews the scientific literature concerning this controversy and presents the results of a recent resource survey of the entire Hawaiian Archipelago that clearly establishes the presence of three species of *Acropora* in Hawaii. These species are *Acropora cytherea*, *A. valida*, and *A. humilis*. Taxonomic descriptions for each species are presented, along with notes on their worldwide geographic distributions. In Hawaii, the three species are found only on six islands in the middle of the chain. Extension of their ranges throughout the archipelago may be limited by discontinuous and sporadic larval recruitment.

THE HAWAIIAN ARCHIPELAGO consists of approximately 132 high volcanic islands, rocky islets, atolls, reefs, banks, shoals, seamounts, and guyots (Armstrong 1973). The island chain stretches northwest from the Island of Hawaii diagonally across the Pacific to Kure Atoll, a distance of 2450 km. Beyond Kure Atoll, a series of drowned atolls (guyots) and seamounts extend the chain to the Emperor Seamounts. The Emperor Seamounts continue northward all the way to the juncture between the Kuril and Aleutian trenches.

In spite of the vast geography of the Hawaiian Archipelago, knowledge of the marine biota of the Hawaiian Islands was, until about 1976, based largely on research done in the major high islands (Hawaii to Niihau). Prior to this time, knowledge of marine flora and fauna of the Northwestern Hawaiian Islands consisted primarily of the results of the United States Exploring Expedition in 1840 and 1841, the "Albatross Expedition" in 1902, and the Tanager Expedition in 1923. In 1976, a five-year research program on wildlife and fisheries management in the Northwestern Hawaiian Islands was planned by the National Marine Fisheries Service, the U.S. Fish and Wildlife Service, the Hawaii State Division of Fish and Game, and the University of Hawaii Sea Grant Program.

In 1978 and 1979, in connection with the five-year research plan, the species composition of coral reefs off the islands of Nihoa, Necker, French Frigate Shoals, Gardner Pinnacles, Maro Reef, Laysan, Lisianski, Pearl and Hermes, Midway, and Kure was surveyed. This inventory confirmed and documented the presence of the coral genus *Acropora* in Hawaii. Three species were recorded. Until this discovery, a controversy over the occurrence of *Acropora* in Hawaii persisted for many years. In part, this controversy was due to the presence in Hawaii of *Acropora* in the geological record from the Miocene followed by apparent disappearance during the Pleistocene. Thus, the purpose of Part 1 of this paper is to summarize the scientific record of the genus in Hawaii, substantiate the taxonomic position of the three species discovered, and describe their present patterns of distribution and

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abundance. In Part 2 of this paper, zoogeographic aspects of *Acropora* are considered.

METHODS

Stations were selected off all major islands or reefs in the Hawaiian Archipelago. At each station, the species composition and community structure of macrobenthic species (> 2 cm in the greatest dimension) were quantitatively analyzed by conducting 25-m or 50-m line transects at depths between 5 and 15 m (Grigg and Dollar 1980). Qualitative estimates of abundance of the macrobenthos covering much larger areas (about 5000 m^2) were also collected. The number of stations selected per island ranged between two and eight, depending proportionately on island size and diversity of habitats. Where present, fragments from mature (largest) colonies of *Acropora* were collected and preserved in formalin. The reproductive condition of these colonies was determined by directly examining the mesentaries of decalcified specimens (Grigg and Boucher, ms) and by standard histological techniques. All samples used to determine reproductive condition were collected in the months of June, September, and November. At one station at French Frigate Shoals, a core was obtained from a water depth of 10 m to ascertain the presence of *Acropora* in the recent past. Material from the core was dated using radiocarbon dating.

The taxonomic position of the three species of *Acropora* was determined from colonies collected in 1978 and 1979 at French Frigate shoals. The Hawaiian specimens were compared with a large number of *Acropora* corals collected from the Great Barrier Reef. (The latter were collected by John Veron and Carden Wallace for a revision of the family Acroporidae.) Type material of *A. variabilis* Klunzinger was received on loan from the Museum für Naturkunde, Humboldt University, Berlin. Radial corallites are illustrated by scanning electron micrographs taken at James Cook University, Australia. The terminology used in this paper is defined by Wallace (1978).

SCIENTIFIC RECORD

The protean reef coral genus *Acropora*, with some 325 nominal species, is one of the most widely distributed of living reef corals in the Indo-Pacific, but its current presence in Hawaiian waters has long been doubted. Its absence from early collections of recent Hawaiian corals was notable. J. D. Dana, in the first (1872) and subsequent editions of his *Corals and Coral Islands*, suggested that the "Hawaiian Islands ... are outside of the Torrid Zone ..., and the corals are consequently less luxuriant and much fewer in species. There are no Madrepores [*Acropora*] and but few of the Austraea and Fungia tribes, while there is a profusion of coral of the hardier genera, *Porites* and *Pocillopora*." Earlier, in 1846, in his great report on the zoophytes of the U. S. Exploring Expedition, Dana pointed out that "at the Sandwich Islands, which are near the northern limits of the coral seas, *Porites* and *Pocillopora* prevail...." Quelch, in his monograph of the *Challenger* reef corals (1886), observed that "it is a noteworthy peculiarity of the coral fauna of the Sandwich Islands that no representative of the widely distributed genus *Madrepora* [*Acropora*] is found on the reefs." But Brook, in his 1893 monograph of the genus, listed the Sandwich Islands as one of the several localities of *Madrepora echinata* Dana, although he listed only three specimens of the species in the British Museum collections, none of them from Hawaii.

For nearly a century there have been on exhibit in the vitrines of the Galérie de Zoologie, Muséum Nationale d'Histoire Naturelle, Paris, two specimens of *Acropora* labelled "*Madrepora longicyathus* M. E. & H. Iles Sandwich. M. Ballieu 1874," on the shell of a large *Pinctada* and "*Madrepora durvillei* M. E. & H. Iles Sandwich. M. Ballieu 1875." These were "discovered" in 1978 by Dennis M. Devaney, the curator of invertebrates at the Bishop Museum in Honolulu, Hawaii. To an inquiry concerning their origin, J. P. Chevalier replied that he could find no record of their acquisition and that M. Ballieu was unknown to the Museum.

He also pointed out in correspondence "a curious thing: besides this sample, there is another example of *Acropora longicyathus* which is fixed also on a shell of oyster (*Pinctada*) but it comes from Tahiti (coll. Cloué, no. 1, 1871)." Like Studer's *M. echinata*, also attached to a pearl oyster shell, it is probable that M. Ballieu's corals were either purchased in Hawaii or were obtained in Tahiti but were mistakenly attributed to Hawaii.

In 1875, when the *Challenger* stopped in Honolulu, Moseley noted (as Verrill did later) that corals not from Hawaiian waters were offered for sale: "There is a large shop of Chinese and Japanese curiosities, and two photographers' shops, where corals, imported mostly from the Marquesas, and spurious imitations of native implements manufactured for sale, are disposed of, at exorbitant prices to passengers from the mail steamer" (Moseley 1879:456).

The first published evidence of the presence of *Acropora* in Hawaii came in 1901 when Studer described some corals in the collections of the Berne Museum, including some collected in 1896 and 1897 by H. H. Schauinsland at Laysan. Among the Hawaiian species were several not previously recorded and still not known to occur in the islands: *Madrepora* (*Acropora*) *echinata* (non Pallas), *Fungia* (*Fungia*) *fungites* (Linn.), *Fungia* (*Ctenactis*) *echinata* (Pallas), *Halomitra tiara* (= *H. pileus* [Linn.]) and *Merulina regalis*? Dana. However, there is no certainty that all of these actually came from Hawaii. Studer noted that at least two had been purchased in Honolulu and thought that they had probably come from elsewhere in the Pacific. His figured specimen of *A. echinata*, a small colony on a large pearl shell, if it did come from Hawaii, is possibly this species but is different from all three species discussed in the present paper. A year later Verrill (1902) said that *A. echinata* was "probably imported," and that he had never seen an authentic species of *Acropora* from Hawaii. Local collectors assert that the genus does not occur there. But great quantities of corals, etc., are brought from the Polynesian Islands to Honolulu by missionary vessels and sold there as curiosities ... and probably this is the case with the several [actually one] species of *Acropora* recorded from the Hawaiian Islands by Brook. Their occurrence there certainly needs confirmation, for in the large authentic collections of corals I have studied from those islands no *Acropora* has occurred.

Studer's specimen was figured again by Vaughan in his monograph on the Hawaiian corals (1907) with no comment on its provenance, save that "this species has been reported from the Hawaiian Islands by Brook and Studer. I have seen no specimens of it from there." Later (1910) he apparently accepted it: "*Acropora* is possibly but not probably, except for *A. echinata*, entirely absent from Hawaii." Notwithstanding the very dubious specimen of *A. echinata*, it has since been accepted that the genus is not found in the Hawaiian coral fauna, the nearest occurrence being at Johnston Island, 720 km to the southwest, where there are at least five species. Dana's 1872 statement has also been accepted as sound, although as late as 1943 Vaughan and Wells pointed out that a number of tropical Pacific coral genera were lacking in Hawaii, and that "*Acropora* is doubtfully represented by a single species."

In 1936, a sizable colony of *Acropora*, probably *A. cytherea* (Dana), was collected at French Frigate Shoals northwest of the main islands. About that time, in Washington, D.C., Paul Galtsoff told John Wells of the find but said that its whereabouts were unknown. In 1946, C. H. Edmondson published a photograph of this specimen in his *Reef and Shore Fauna of Hawaii*. In reply to an inquiry in 1947 about the specimen, he wrote that it was not in the Bishop Museum, and that "the Hawaiian boys who collected it did not inform me of its disposition." Was it broken up and sold for souvenirs? A search at the National Museum of Natural History failed to find any record. Nevertheless, this lost coral was clear evidence of the presence of living *Acropora* in the Hawaiian Islands, and indicated that further search at French Frigate Shoals would provide a final answer.

Nearly 40 years later, an *Acropora* colony was found living at a depth of 40 ft off Poipu on the south coast of Kauai. R. A. Kinzie III sent it to John Wells, who tentatively

identified it as *A. paniculata* Verrill, known from one or two localities in the western Pacific. It was later figured (Maragos 1977) with notes on its origin.

Then, in 1977 came the major discovery of Hawaiian *Acropora*. John Naughton found a tabulate colony about 2 ft across at La Perouse Pinnacles, French Frigate Shoals, some 500 miles northwest of Kauai. The colony was subsequently determined to be *A. cytherea*. More colonies were located by Leighton Taylor. In 1978 and 1979, R. W. Grigg found still more *A. cytherea* and two other species, *A. valida* and *A. humilis*, the first two in relatively large numbers at depths ranging from 3 to 20 m at a variety of localities at French Frigate Shoals. This dispelled any idea that *Acropora* is a rare Hawaiian coral and initiated the present paper.

TAXONOMY

The three species of *Acropora* in Hawaii identified from specimens collected at French Frigate Shoals are *A. cytherea* (Dana), *A. valida* (Dana) (= *A. variabilis*), and *A. humilis* (Dana). All of these species have broad Indo-Pacific distributions, and all occur in some locations of the type dubbed "marginal belts" by Crossland (1949), characterized by "absence or almost absence of the great reef builder, the genus *Acropora*."

Unfortunately, with knowledge of the biology of *Acropora* in a poor state, it is not possible to discuss special life-history strategies of these species which might explain their broad distribution. However, all can be associated with either severe or unpredictable conditions. *A. cytherea* is known on the Great Barrier Reef (mainly from unpublished observations) as one of the plate-forming species which are early colonizers of disturbed areas. *A. valida* characteristically occurs as the dominant (and sometimes the only) *Acropora* in the austere conditions of the algal ridge (e.g., in the Marshall Islands). Similarly *A. humilis* is a dominant (or codominant) coral on windward reef fronts receiving extreme wave action on the Great Barrier Reef.

Acropora cytherea (Dana, 1846)

Madrepora cytherea Dana, 1846:441, pl. 32, fig. 3a, 3b; Brook 1893:99 (synonymy).
Acropora cytherea: Crossland 1952:215; Wallace 1978:289, pls. 63, 64A, 64D, 66C, 66D, 67.
Madrepora efflorescens Dana, 1846:441, pl. 33, fig. 6; Brook 1893:35 (synonymy).
? *Acropora efflorescens*: Pillai and Scheer 1976:26, pl. 3, fig. 3.
Madrepora armata Brook, 1892:452; 1893:100, pl. 10, figs. A, B (synonymy).
Madrepora reticulata Brook, 1892:461; 1893:68, pl. 4, figs. A, B.
Madrepora reticulata var. *cuspidata* Brook, 1893:69.
Acropora reticulata: Wells 1954:422, pl. 110, figs. 4–6, pl. 114, figs. 1–6 (synonymy); Pillai and Scheer 1976:28, pl. 7, fig. 1.
Madrepora arcuata Brook, 1893:102, pl. 12; Studer 1901:395.
Acropora cytherella Verrill 1902:253, pl. 36, fig. 7, pl. 36a, fig. 7, pl. 36f, fig. 1 (synonymy).
Acropora corymbosa "*cytherea* Form": von Marenzeller 1907:32, pl. 1, figs. 1, 2, pl. 2, fig. 3.
Acropora hyacinthus (part): Hoffmeister 1925:64; Wells 1954:421.

MATERIAL EXAMINED: 4 specimens collected at French Frigate Shoals, July 1979.

DESCRIPTION: This species occurs as stalked tables, up to 480 cm in diameter, with a more or less rounded outer edge, sometimes with additional platelike layers. Color is pale brown.

SKELETON: The specimens are all portions of flat plates (figure 1*a*). The primary direction of branching is horizontal and there is considerable, but not complete, anastomosis of horizontal branches. From these branches, short vertical to oblique branchlets mainly 5–10 mm in length arise singly or in groups (figure 1*b*). The radial corallites are appressed tubular with the outer wall extended upward as a lip. Many radial corallites are in transition to axial corallite status, and these

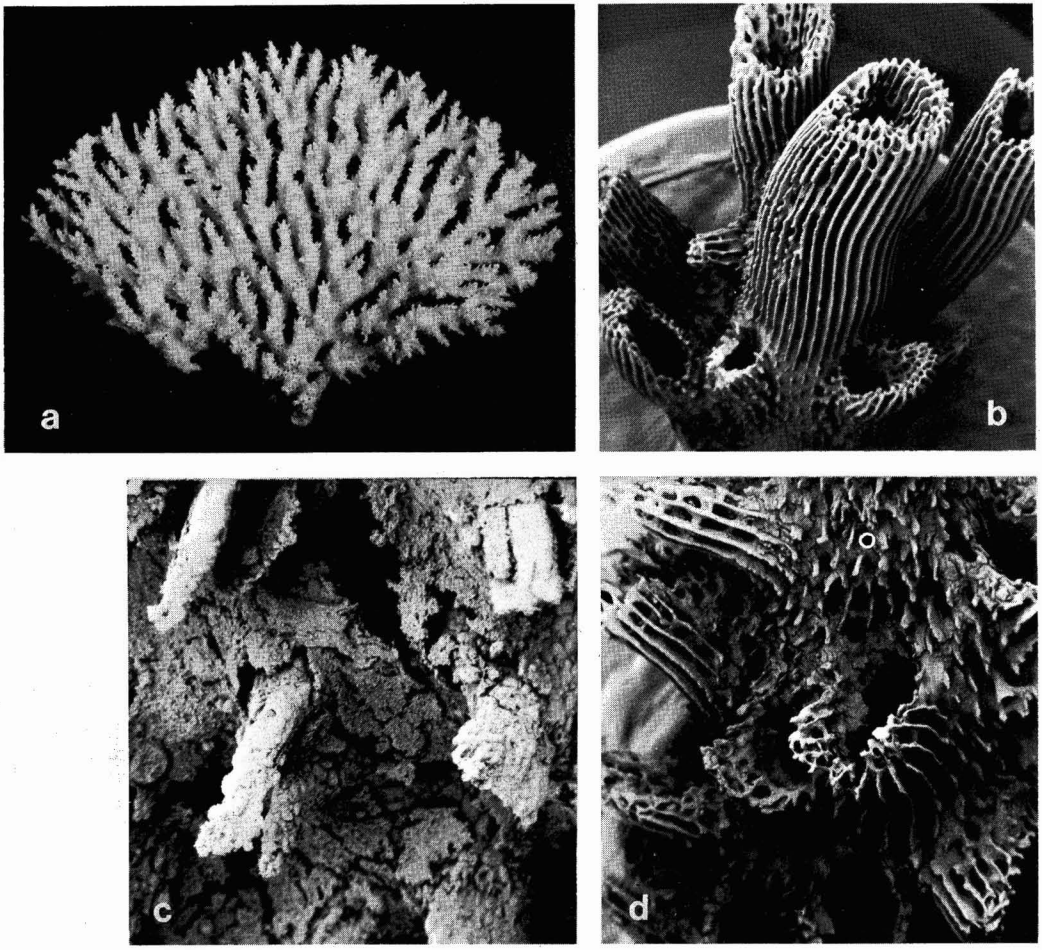

FIGURE 1. *Acropora cytherea: a*, general view, 0.5×; *b*, S.E.M. of branchlet bundle, 8×; *c*, S.E.M. of coenosteum between corallites, 180×; *d*, S.E.M. of radial corallites, 18×.

appear tubular with dimidiate openings. The axial corallites are usually 2–5 mm exert. Their outer diameter is 1.5–2.5 mm, inner diameter 0.6–1.2 mm. The primary septa are all present, up to $\frac{1}{3}$R; the secondary cycle is absent, or occasionally 1–3 septa are just visible. The coenosteum is costate on radial corallites and reticulate with scattered, laterally flattened spines elsewhere (Figure 1*c*, *d*).

DEPTH RANGE AT FRENCH FRIGATE SHOALS: 3–20 m.

GEOGRAPHIC DISTRIBUTION: Madagascar (Pichon, personal communication), Mascarene Archipelago (Faure 1977), Amirante Islands, Seychelles, Maldives, Minicoy, Arafura Sea, China Sea, Great Barrier Reef, Solitary Islands, Funafuti Atoll, Fiji Islands, Marshall Islands, Tahiti, Northwestern Hawaiian Islands, Hawaii.

DISCUSSION: This is a common reef-front species, sometimes referred to as *A. reticulata*, a synonym, and sometimes confused with *A. hyacinthus*. On many reefs *A. hyacinthus* and *A. cytherea* have overlapping distributions, with the former shallower than the latter. *A. hyacinthus* does not have the long axial corallites of *A. cytherea*; its radial corallites have more rounded lips and are more evenly arranged on branchlets. There is a slight possibility that some of the table colonies at French Frigate Shoals are *A. hyacinthus*.

Acropora valida (Dana, 1846)

Madrepora valida Dana, 1846:461, pl. 35, fig. 1; Brook 1893:168.
Acropora valida: Hoffmeister 1925:60, pl. 12, figs. 1, la–c; Wells 1954:429, pl. 130, figs. 7–9; Nemenzo 1967:99, pl. 30; Pillai and Scheer 1976:29, pl. 7, figs. 3, 4; Zou Ren-lin 1978:107.
Madrepora variabilis Klunzinger, 1879:17, pl. 1, fig. 10, pl. 2, figs. 1, 5, pl. 5, figs. 1, 3, pl. 9, fig. 14; Brook 1893:161.
Acropora variabilis: von Marenzeller 1907:49, pl. 15, figs. 40–44; Vaughan 1918:181, pl. 80, figs. 2, 3, 3a, 3b; Faustino 1927:276; Wells 1950:38; 1954:428, pl. 128, figs. 1, 2, pl. 130, figs. 1, 2; Rossi 1954:52; Stephenson and Wells 1956:19; Scheer and Pillai 1974:23, pl. 8, fig. 2; Pillai and Scheer 1976:31; Zou Ren-lin 1978:107; Wallace 1978:299, pl. 80C, D.
Acropora variabilis var. *pachyclados* Klunzinger: Crossland 1952:222, pl. 38, figs. 1, 6.

MATERIAL EXAMINED: 5 specimens, collected at French Frigate Shoals, July 1979.

DESCRIPTION: This species is corymbose in growth form (Figure 2*a*). Colonies up to 30 cm high and 40 cm wide occur at French Frigate Shoals. Color is tan.

SKELETON: From a central attachment area, branches arise vertically to obliquely, sometimes branching again, and sometimes proliferating at the tip. Branches are 7–12 mm greatest diameter, up to 70 mm in length, and only slightly tapering. Radial corallites are of mixed length, or mainly all of similar length, up to 5 mm long, partly to fully appressed tubular (Figure 2c). The openings are oval, directed at 45° to 90° to the branch, the outer edge of the wall sometimes extends upward and is slightly liplike. Primary septa are all present, usually up to $\frac{1}{3}$R, but sometimes to $\frac{1}{2}$R; the secondary cycle is partly to fully present, up to $\frac{1}{4}$R. Axial corallites are around 1 mm exert, with outer diameter 2.0–2.8 mm, inner diameter 1.0–1.3 mm. Primary septa are present, up to $\frac{1}{2}$R; secondary septa are absent, or 1 to 3 present, to less than $\frac{1}{4}$R. The coenosteum consists of lines of laterally flattened spines (Figure 2b).

DEPTH RANGE AT FRENCH FRIGATE SHOALS: 3–20 m.

GEOGRAPHIC DISTRIBUTION: Madagascar (Pichon, personal communication), Mascarene Archipelago (Faure, personal communication), Red Sea, Maldives, Andamans, Nicobar Island, Mergui Archipelago, Singapore, Philippines, China Sea, Great Barrier Reef, Solitary Islands (Veron et al. 1974), Fiji Islands, Marshall Islands, New Caledonia, Tonga, Tuamotus, Northwestern Hawaiian Islands.

DISCUSSION: The two species *A. valida* (type locality, Fiji Islands) and *A. variabilis* (type locality, Red Sea) are here combined for the first time, as the relatively little-treated species *A. valida* falls well within the large range of variability recorded for *A. variabilis*. The French Frigate Shoals specimens are similar in all characteristics, except the inner axial corallite diameter, to some specimens from the Palm Island group, Great Barrier Reef.

Acropora humilis (Dana, 1846)

Madrepora humilis Dana, 1846:483, pl. 31, fig. 4, pl. 41, fig. 4.
Acropora humilis: Wells 1954:425, pl. 100, fig. 1, pl. 126, figs. 1–6, pl. 127, figs. 3, 4, pl. 128, figs. 3–5 (synonymy). Rossi 1954:50; Stephenson and Wells 1956:15; Scheer 1967:424, figs. 4, 5; Pillai and Scheer 1976:32; Zou Ren-lin 1978:105; Wallace 1978:300, pls. 81, 82, 83. (For a complete synonymy refer to Wells 1954.)

MATERIAL EXAMINED: 1 specimen collected at French Frigate Shoals, 8 m depth, July 1979.

DESCRIPTION: The specimen examined comprises small pieces from a corymbose or caespitose colony (Figure 3*a*). The longest branch is 55 mm in length, and the broadest 22 mm. Radial corallites are mixed sizes, up to 3 mm diameter and 3 mm in length,

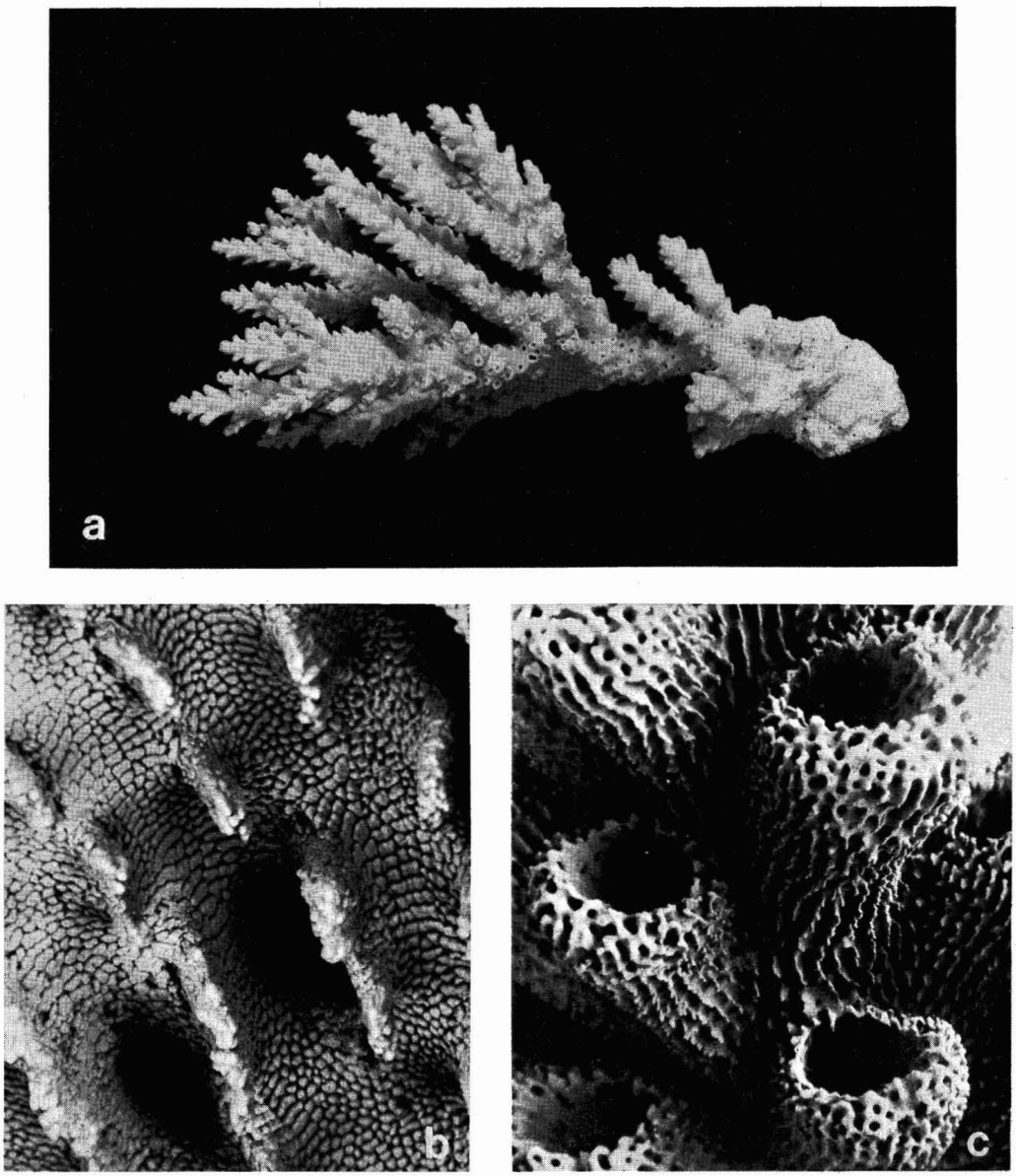

FIGURE 2. *Acropora valida: a*, general view, 0.7×; *b*, S.E.M. of coenosteum between corallites, 16×; *c*, S.E.M. of radial corallites, 160×.

projecting at 90° to branch, tubular with dimidiate openings and thickened walls (Figure 3*b*). Axial corallites are 1.5 mm exert, 4.0–5.5 mm outer diameter, 1.0–1.5 mm inner diameter. Both septal cycles are developed, primaries to $\frac{1}{2}$R, secondaries to $\frac{1}{4}$R. Coenosteum is a dense arrangement of costae on radial corallites, with lines of laterally flattened spines between radial corallites.

GEOGRAPHIC DISTRIBUTION: Madagascar (Pichon 1978), Mascarene Archipelago (Faure 1977), Red Sea, Arafura Sea, Maldives, Cocos-Keeling, Philippines, China

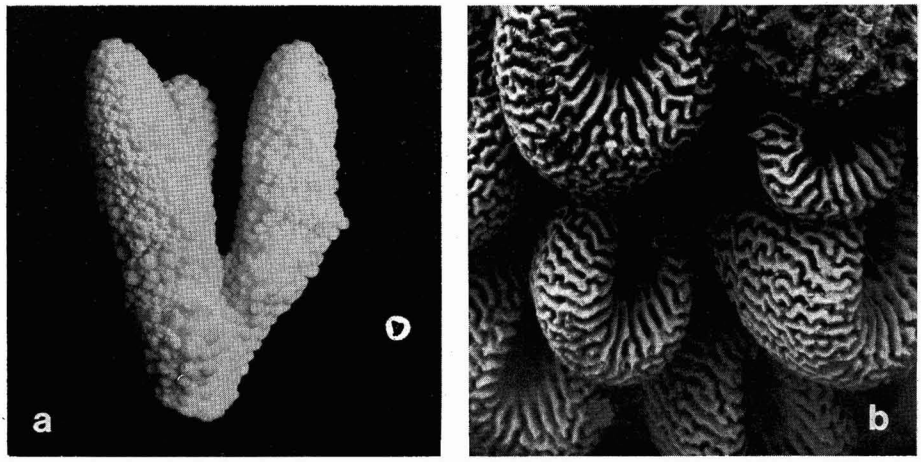

FIGURE 3. *Acropora humilis: a*, general view, 1×; *b*, S.E.M. of radial corallites, 16×.

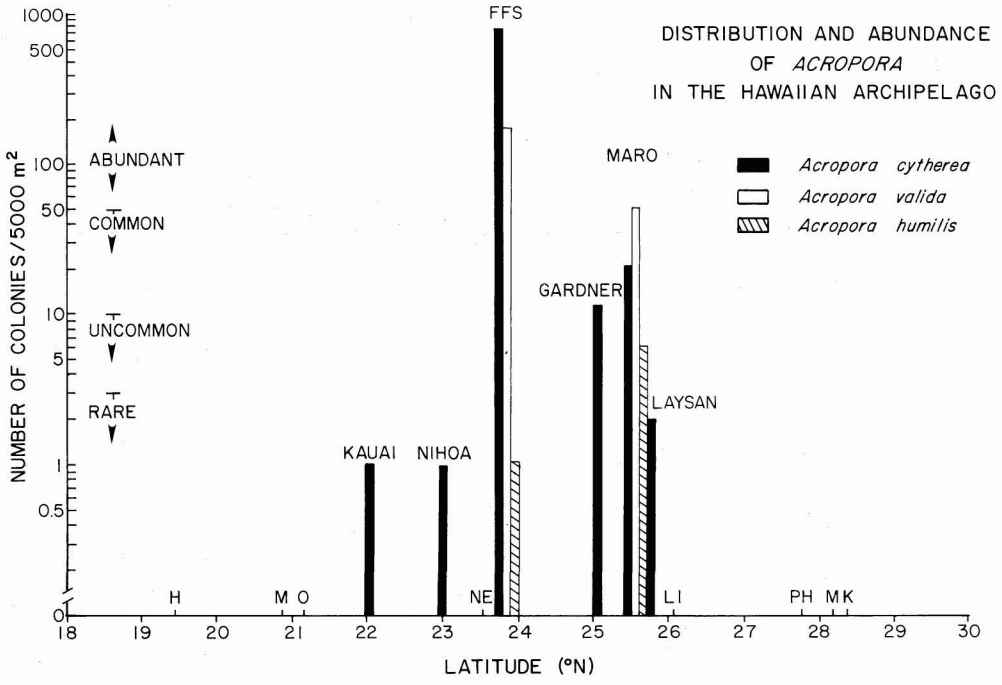

FIGURE 4. Distribution and abundance of *Acropora* spp. in the Hawaiian Archipelago in the most favorable habitats. Note that abundance is expressed on a log scale. This is done to emphasize the importance of one colony, that is, the capability of colonization. Only one colony of *A. cytherea* was found on Kauai and Nihoa and two on Laysan, clearly setting the outer limit of the distribution. The center of the distribution is French Frigate Shoals, where over 1000 colonies of *A. cytherea* can be found in a 5000 m^2 area.

Sea, Great Barrier Reef, Solitary Islands (Veron 1974), Solomon Islands, Samoa, Fiji, Marshall Islands, Tuamotus, French Frigate Shoals, Hawaii.

DISCUSSION: This species, as revised by Wells (1954), has a long list of synonyms. Studies underway on the Great Barrier Reef suggest that this lumping may be too extreme, and that two, or even three, species may be involved. However, there is no doubt that the French Frigate Shoals material is the same species as *A. humilis s. s. A. humilis* is characteristically a shallow-water *Acropora* occurring as a dominant species on outer reef flats and the upper few meters of exposed reef fronts, but it does also occur commonly on horizontal reef surfaces that are subtidal and not exposed to strong wave action. In the first situation, colonies tend to have a broadly encrusting base (of a similar diameter to the corallum) from which branches arise vertically with little or no secondary branching (e.g., see Wells 1954, pl. 128, fig. 5; Morton 1974, fig. 10D; Wallace 1978, pl. 81A). In the second, the attachment diameter is smaller than that of the corallum, and secondary branching is more frequent (e.g., see Wallace 1978, pl. 81B). The French Frigate Shoals material is in the second category.

DISTRIBUTION, ABUNDANCE, AND REPRODUCTIVE BEHAVIOR

The results of coral reef surveys off all major islands in the Hawaiian Archipelago indicate that species of *Acropora* occur on only six islands (Kauai, Necker, French Frigate Shoals, Gardner Pinnacles, Maro Reef, and Laysan, Figure 4). Three species of *Acropora* were found at French Frigate Shoals and Maro Reef, whereas only one was collected at Kauai, Necker, Gardner Pinnacles, and Laysan islands. The distributional center for all three species appears to be at French Frigate Shoals, where they are most abundant (Figure 4). *A. cytherea* and *A. valida* are about three times more abundant at French Frigate Shoals than at Maro Reef. In some localities at French Frigate Shoals, *A. cytherea* occupies an average of 40 percent of the bottom cover (Figure 5). The largest colonies of *A. cytherea* measured at French Frigate Shoals are 480 cm in diameter.

At French Frigate Shoals *A. cytherea* occurs between depths of 3 and 20 m in many habitats: inside the lagoon on patch reefs, in areas partially protected from open sea, and off all exposed sides of the island. The most well-developed colonies occur at the southwestern end of the "atoll" near Disappearing Island. *A. valida* occurs in more restricted habitats partially protected from open sea but at similar depths. One colony of *A. humilis* was found at French Frigate Shoals inside the barrier reef at a depth of 10 m. Several other colonies of *A. humilis* were found at Maro Reef also near 10 m depth. Of the three species of *Acropora* in Hawaii, only *A. cytherea* has a variable growth form dependent upon habitat. Inside the barrier reef, vasiform colonies of *A. cytherea* grow higher off the bottom with taller and narrower supporting basal stalks than colonies outside the reef. Colonies in areas exposed to open sea are more heavily branched and thicker than colonies in protected habitats.

The distributional patterns of all three species are very patchy. For example, the sighting of one colony during a survey would invariably increase the probability of finding another colony of the same species. Aggregation could result from gregarious larval behavior or immediate settlement or could be due to physical fragmentation. At French Frigate Shoals many settlement sites can be distinguished, hence larval settlement must occur from time to time. Even so, larval recruitment may not be a continuous process. The size frequency distribution of *A. cytherea* is relatively continuous, suggesting low year-class variability; however, this could also be a result of frequent fragmentation. In June 1978, 36 colonies of *A. cytherea* at 10 m adjacent to La Perouse Pinnacle were measured and tagged in order to determine growth. In September 1979, the same area was resurveyed, but only 16 tagged colonies could be found. It was evident that many colonies in this area had

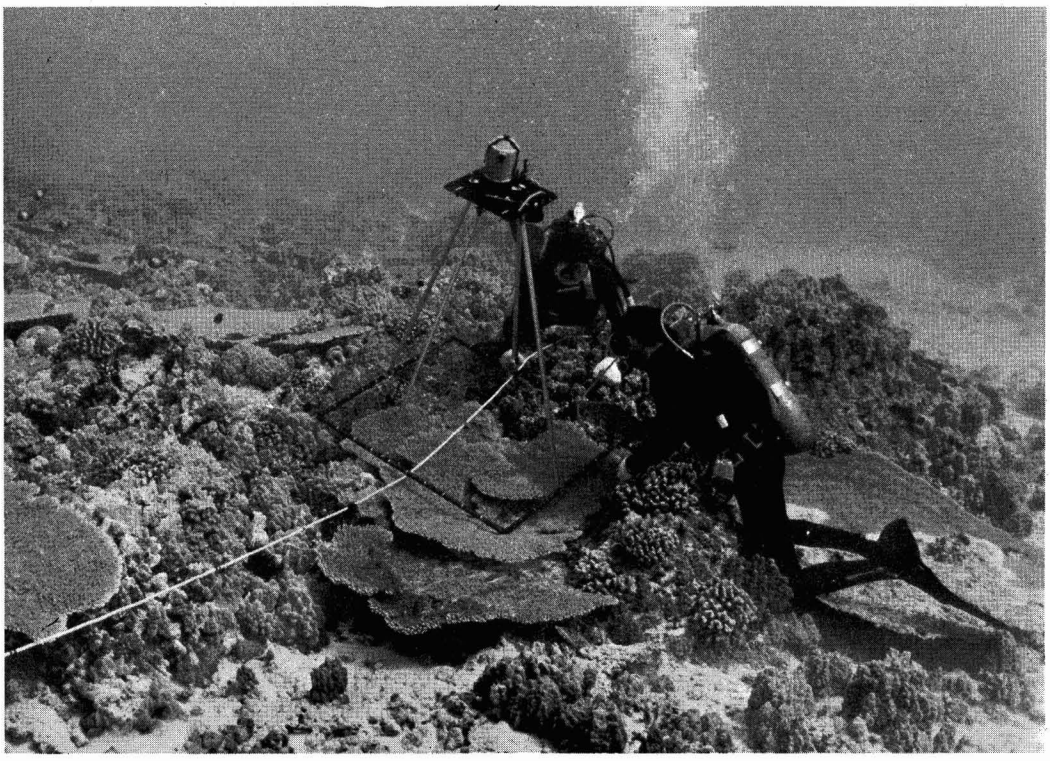

FIGURE 5. Benthic photo-transect conducted at French Frigate Shoals at 10 m depth on the outer reef south of Disappearing Island. In this area *Acropora cytherea* accounts for 40% of the bottom cover.

been fragmented or overturned. In January 1979, a severe "Kona" storm hit this portion of the archipelago and may have caused the observed destruction. In any case, it would appear that the aggregated patterns of distribution for both *A. cytherea* and *A. valida* are due to both fragmentation and larval behavior, at least at French Frigate Shoals.

In order to determine the degree to which larval settlement within the archipelago is due to local reproduction versus outside recruitment, colonies of *A. cytherea* and *A. valida* were collected at French Frigate Shoals, Maro Reef, and Laysan Island during as many months of the year as possible. Each collection consisted of fragments broken from the largest (most mature) colonies present. The mesenterial septa of polyps from these colonies were examined and all oocytes and spermaries were measured. Unfortunately, the results are inconclusive, primarily because the data cover too few months to detect whether or not an annual cycle exists or whether or not gonadal material in colonies from these islands ever reaches reproductive maturity (Table 1).

The largest oocyte or spermary recorded in the three species of *Acropora* on any Hawaiian island was 410μ in *A. cytherea*, 240μ in *A. valida*, and 250μ in *A. humilis* (Table 1). Recent work in Australia by Carden Wallace and Jamie Oliver (personal communication) on reproductive cycles of *Acropora* indicates that mature or near-mature colonies of *A. cytherea* contain oocytes up to 934μ in length and spermaries up to 1321μ in length. Equivalent measures for *A. valida* are 1280μ for oocytes and 3280μ for spermaries. These data leave little doubt that all the colonies examined in Hawaii of at least these two species, and probably of *A. humilis* as well, were in an immature state. Since the Hawaiian data were collected over a six-month time period

TABLE 1

REPRODUCTIVE CONDITION OF *Acropora* spp. IN THE NORTHWESTERN HAWAIIAN ISLANDS

SPECIES AND LOCATION	MONTH COLLECTED	NUMBER COLONIES COLLECTED	NUMBER POLYPS EXAMINED	PERCENT POLYPS WITH GONADS	OOCYTE LENGTH (μm)	SPERMARY LENGTH (μm)
Acropora cytherea						
FFS*	Sept. 1980	20	64	44%	n = 45 $\bar{x}$ = 106 SD = 44.5 Range = 35–300	n = 40 $\bar{x}$ = 126 SD = 36.9 Range = 80–220
FFS	Nov. 1978	4	21	100%	n = 82 $\bar{x}$ = 238 SD = 83.4 Range = 110–440	n = – $\bar{x}$ = – SD = – Range = –
Maro	June 1979	7	32	0%	n = – $\bar{x}$ = – SD = – Range = –	n = – $\bar{x}$ = – SD = – Range = –
Laysan	June 1979	1	10	0%	n = – $\bar{x}$ = – SD = – Range = –	n = – $\bar{x}$ = – SD = – Range = –
Laysan	Sept. 1980	1	10	10%	n = – $\bar{x}$ = – SD = – Range = –	n = 2 $\bar{x}$ = 100 SD = 0 Range = –
Acropora valida						
FFS	June 1979	2	15	93%	n = 85 $\bar{x}$ = 72 SD = 46.5 Range = 15–240	n = 2 $\bar{x}$ = 110 SD = 70.7 Range = 60–160
Maro	Sept. 1980	20	65	7%	n = 18 $\bar{x}$ = 58 SD = 26.0 Range = 30–110	n = – $\bar{x}$ = – SD = – Range = –
Acropora humilis						
Maro	Sept. 1980	6	24	62%	n = 40 $\bar{x}$ = 128 SD = 56.0 Range = 50–250	n = 3 $\bar{x}$ = 153 SD = 50.3 Range = 60–200

* French Frigate Shoals

(June, September, November), it would be surprising but not impossible to have missed the season in which reproductive maturity occurs in all three species. On the basis of existing data it therefore appears unlikely that species of *Acropora* in Hawaii successfully produce larvae. Recruitment may depend entirely on recolonization from outside the archipelago. If this conclusion is correct, the patterns of distribution and abundance of *Acropora* in Hawaii should reflect the present route of colonization (see *Acropora* in Hawaii. Part 2. Zoogeography).

Observations at Gardner Pinnacles (midway between French Frigate Shoals and Maro Reef) may shed further light on the question of the source and frequency of larval recruitment in the Hawaiian Archipelago. At Gardner Pinnacles in 1978, most of the reef at 10 m depth was dominated by very large (1–10 m diameter) but dead colonies of *A. cytherea*. Only three living colonies were sighted in 1978, all less than 4 cm in diameter. On the surface of the dead colonies of *A. cytherea*, the largest colonies of *P. lobata* that were present were collected

($n = 10$) and later sectioned in the laboratory so that growth bands could be counted (Buddemeier, Maragos, and Knutson 1974; Grigg and Dollar 1980). The oldest colonies were 16 years, suggesting that some catastrophic event prior to 1962 killed all of the *A. cytherea* at Gardner. Since that time, the only successful recruitment appears to have been in the last year or two. Either survival of recruits at Gardner Pinnacles is very low or recruitment is a very sporadic process (on the order of once in 15 years). This may explain why *Acropora* spp. have not dispersed to more islands in the chain. If the source of recruitment is within the chain (if the center of distribution is French Frigate Shoals), the Gardner data suggest that reproduction is sporadic, possibly only in very warm years. Alternatively, recruitment may depend entirely on sporadic colonization from outside the archipelago.

While recruitment of *Acropora* in Hawaii may be discontinuous and severe mortality may be intermittent, it appears as though *Acropora* has been in Hawaii for some time. In 1979, two 50-cm cores, 5 cm in diameter, were extracted from the reef at a depth of 10 m at French Frigate Shoals. At the bottom of one of the cores was a piece of fossil coral identified as *Acropora* (Michel Pichon, personal communication). Unfortunately this piece of coral was unsuitable for radiocarbon dating due to a high calcite content. However, directly above the *Acropora* there was an intact fragment of *Porites* suitable for radiocarbon dating. The radiocarbon age of this fragment is 414 $\pm$ 68 years. This is clear evidence that *Acropora* has been in Hawaii since before the time of Western contact (1778). The zoogeographic implications of this finding coupled with the data on reproduction, ecology, and possible recruitment from outside the archipelago are sufficiently complex to warrant separate treatment and therefore are considered in Part 2 of this paper.

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LITERATURE CITED

ARMSTRONG, R. W., ed. 1973. Atlas of Hawaii. University of Hawaii Press, Honolulu. 222 pp.

BROOK, G. 1893.The genus *Madrepora*. Cat. Madrep. Corals, Br. Mus. (Nat. Hist.), vol. 1.

BUDDEMEIER, R. W., J. E. MARAGOS, and J. W. KNUTSON. 1974. Radiographic studies of reef coral exoskeleton. 1. Rates and patterns of coral growth. J. Exp. Mar. Biol. and Ecol. 14:179–200.

CROSSLAND, C. 1949. Reef corals of the South African coast. Ann. Natal Mus. 11(2):169–203, 14 pls.

DANA, J. D. 1846. Zoophytes. U.S. Expl. Exped., vol. 7.

DANA, J. D. 1872. Corals and coral islands. New York.

EDMONDSON, C. H. 1946. Reef and shore fauna of Hawaii. Bernice P. Bishop Mus. Spec. Publ. 22.

FAURE, G. 1977. Annotated check list of corals in the Mascarene Archipelago, Indian Ocean. Atoll Res. Bull. 203:1–26.

GRIGG, R. W., and S. J. DOLLAR. 1980. The status of reef studies in the Hawaiian Archipelago. *In* R. W. Grigg and R. Pfund, eds. Proceedings of the Symposium on Status of Resource Investigations in the Northwestern Hawaiian Islands. UNIHI-SEAGRANT-MR-80-04.

GRIGG, R. W., and L. BOUCHER. A new method to assess reproductive condition in corals. Manuscript.

MARAGOS, J. E. 1977. Order Scleractinia. *In* Reef and shore fauna of Hawaii. 1. Protozoa through ctenophora. Bernice P. Bishop Mus. Spec. Publ. 64(1):158–241.

MARSHALL, S. M., and T. A. STEPHENSON. 1933. The breeding of reef animals. Part 1. The Corals. Gt. Barrier Reef Exped. 1928–29. Sci. Rep. 3(8):219–245.

MORTON, J. 1974. The coral reefs of the British Solomon Islands: a comparative study of their composition and ecology. Proc. 2d Int. Symp. On Coral Reefs 2: 31–53.

MOSELEY, H. N. 1879. Notes by a naturalist on the *Challenger*.... Macmillan, London.

PICHON, M. 1978. Recherche sur les peuplements à dominance d'althozoaires dans les récifs coralliens de Tuléar (Madagascar). Atoll Res. Bull. 222:1–446.

QUELCH, J. J. 1886. Report on the reef corals. Challenger Reports, Zoology, vol. 16.

RINKEVICH, B., and Y. LOYA. 1979. The reproduction of the Red Sea coral *Stylophora pistillata*. 1. Gonads and planulae. Mar. Ecol. Prog. Ser. 1:133–144.

STUDER, T. 1901. Madreporarier von Samoa, den Sandwich-inseln und Laysan. Ergebnisse einer Reise nach dem Pacific (Schauinsland 1896–1897). Zool. Jahrb. Syst. 14:388–428.

VAUGHAN, T. W. 1907. Recent Madreporaria of the Hawaiian Islands and Laysan. Proc. 7th Int. Zool. Congr. Boston. 12 pp.

VAUGHAN, T. W. 1910. Review of: J. S. Gardiner, Flora and fauna of the Maldive and Laccadive Islands, vol. 2, suppl. 1, Madreporaria, parts 3 and 4. Science 21:984–985.

VAUGHAN, T. W., and J. W. WELLS. 1943. Revision of the suborders, families and genera of the Scleractinia. Geol. Soc. America, Spec. Pap. 44.

VERON, J. E. N. 1974. Southern geographic limits to the distribution of Great Barrier Reef hermatypic corals. Proc. 2d Int. Symp. on Coral Reefs 1:465–473.

VERON, J. E. N., R. A. HOW, T. J. DONE, L. D. ZELL, M. J. DODKEN, and A. F. O'FARRELL. 1974. Corals of the Solitary Islands, Central New South Wales. Aust. Jour. Mar. Freshwater Res. 25:194–208.

VERRILL, A. E. 1902. Notes on corals of the genus *Acropora* (*Madrepora* Lam.), with new descriptions and figures of types, and of several new species. Conn. Acad. Arts Sci., Trans. 11:207–266.

WALLACE, C. 1978. The coral genus *Acropora* (Astrocoeniinae: Acroporidae) in the central and southern Great Barrier Reef province. Mem. Queensland Mus. 18(2): 273–319, pls. 43–103.

WELLS, J. W. 1954. Recent corals of the Marshall Islands. U. S. Geol. Survey, Prof. Paper, 260–I:385–486.